

Convenors: Nils Chr Stenseth, Grant Singleton and Zhi-Bin Zhang  
n.c.stenseth@bio.uio.no; grant.singleton@csiro.au; zhangzb@panda.ioz.ac.cn

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## RODENT ECOLOGY AND PLAGUE IN NORTH AMERICA

Gary W. Witmer

USDA National Wildlife Research Center 4101 LaPorte Avenue Fort Collins, CO 80521-2154, USA  
Gary.W.Witmer@aphis.usda.gov

### Abstract

Complex rodent communities occupy the western United States. These communities are susceptible to the exotic disease, plague, that has become enzootic in the region since 1899. Weather conditions, the susceptibility of rodent species to plague, population dynamics, and the intra-specific interactions between populations of mammals and their flea associates all contribute to the periodic outbreaks of plague. Understanding these ecological relationships allows managers to generate predictions and to intervene in plague situations so as to reduce the negative effects on ecosystems and to reduce the risk of plague to humans.

### Introduction

The order Rodentia is the largest order of mammals; more than a third of all mammals are rodents. Rodents have evolved to fill a vast array of diverse ecological niches around the world. Rodents fill many important roles in ecosystems, including those that involve dispersal of seed and spores and the consumption and shedding of vegetation—all of which affect the composition, structure, and succession of vegetation as well as nutrient cycling and decomposition. Rodents also mix and aerate soils through their burrowing activities. In addition, they provide an essential prey base for many species of predators. Finally, rodents provide a source of food and furs for humans in some situations.

Unfortunately, in a number of situations on every continent, some species of native or introduced rodents cause significant damage to crops, stored foodstuffs, property, and natural resources. They also may pose a health and safety hazard to humans and their livestock and companion animals. Rodents play a major role in numerous zoonotic diseases around the world, including hantavirus, monkey pox, relapsing fever, leptospirosis, and plague. In this paper, I review the role of rodents in the occurrence of plague in North America. A good understanding of the species involved, their ecology, population dynamics and interactions with other species is essential in predicting, preventing and controlling plague outbreaks.

### Plague in North America

Plague, caused by the bacterium *Yersinia pestis*, is a serious, worldwide zoonosis. Throughout recorded

history, there have been three major plague pandemics in which a total of more than 200 million humans died (Gasper and Watson, 2001). Several thousand human cases occur each year on the continents of Africa, the Americas, and Asia (Gage, 1998). There are three predominant clinical forms of plague: bubonic, septicaemic, and pneumonic (Gage, 1998, Gasper and Watson, 2001). Human plague infection results in fever, headache, chills, myalgia, prostration, malaise, gastro-intestinal symptoms, and often acute lymphadenopathy (Gage, 1998). Although plague can be readily treated with various antibiotics, there is a relatively high mortality rate if treatment is not begun promptly. These bacteria are aggressive at invading lymphoid tissue and good at evading annihilation by the immune system. Although many species of mammals are susceptible to plague, a relatively small number of rodent species are the principal maintenance hosts of plague in plague-endemic areas of the world (Gage, 1998). Exposure to plague is through the bite or scratch of an infected animal, through handling or consuming an infected animal, or more commonly, through the bite of an infected vector—usually a flea.

Plague arrived in several North American shipping ports via rodent-infested ships around 1899 (Antolin *et al.*, 2002). Although plague did not become established near eastern and southeastern United States seaports, it became well established in California and then spread throughout the semi-arid western states. The eastward spread of plague has stopped at about the eastern edge of the short-grass prairie ecosystem. The demarcation line runs roughly north-south from western North Dakota southward through central Texas. About 10–15 human cases of plague occur in

the United States each year (Antolin *et al.*, 2002). The disease occurs to a lesser extent in Canada and Mexico.

### Rodent ecology and role in plague in North America

A large number of native rodent species occur in the western United States; in any given area, there are usually more than 30 species. The species in these complex communities are well adapted to their ecological niches, and competition for limited resources can be keen. With the exception of introduced nutria (*Myocaster coypus*) in aquatic systems in some regions, exotic rodents have not been able to establish themselves (outside of urban-suburban settings) within the native rodent communities.

Several rodent species and their associated flea complexes are maintenance hosts (also called enzootic hosts) for plague and they form the basis of enzootic foci in the western United States. These species include the deer mouse (*Peromyscus maniculatus*), the California vole (*Microtus californicus*), the rock squirrel (*Spermophilus variegatus*), some kangaroo rats (*Dipodomys* spp.), and possibly other species (Antolin *et al.*, 2002; Gage, 1998; Gasper and Watson, 2001). Maintenance hosts are relatively resistant to the disease, and they have a relatively short life cycle and rapid replacement rate, a long polyestrous breeding season, and vector flea activity throughout the year. Antibody detection in host populations can vary from low to virtually 100%.

Many other rodent species are epizootic or amplification hosts with the characteristics of relatively low resistance to plague, high mortality, and rapid spread of the disease through their populations. These species are usually longer lived and monestrous, and the plague outbreaks in their populations are more likely to occur at high population densities. Amplification hosts include many species of ground squirrels (*Spermophilus* spp.), prairie dogs (*Cynomys* spp.), wood rats (*Neotoma* spp.) and chipmunks (*Tamias* spp.), as well as fox squirrels (*Sciurus niger*). Highly social species, such as prairie dogs, are particularly at risk. During plague outbreaks in amplification host populations, there is a higher likelihood of the disease being transmitted to susceptible, non-rodent hosts such as humans, primates, and wild and domestic cats. Finally, in addition to maintenance hosts and amplification hosts, there is a group of resistant non-rodent plague hosts that includes ungulates and most carnivores.

It has been hypothesized that plague outbreaks are initiated by a set of weather conditions that includes

increased rainfall and mild temperatures (Enscoe *et al.*, 2002, Parmenter *et al.*, 1999). These conditions provide increased food resources (plants, insects) for rodents and cause rodent populations to rapidly increase. Moreover, the increased soil moisture and mild temperatures result in greater flea reproduction and survivorship. Temperature also influences a condition in fleas called "blockage," whereby the fleas are more likely to transmit plague while attempting to feed on a host (Gage, 1998, Gasper and Watson, 2001). Perhaps because of increased dispersal of individuals in "crowded" rodent populations, the plague organism has the opportunity to break out of the enzootic cycle and reach epizootic or amplification hosts and, eventually, susceptible non-rodent hosts such as humans. Once rodent populations begin to crash after a plague outbreak, fleas begin a process called "straggling," whereby their regular host is not available, so fleas seek alternative hosts, and thus they amplify the spread of the disease to other species (Gasper and Watson, 2001). Additionally, carnivores, ungulates, birds, and other wildlife may play a role in this disease cycle by transporting plague-infected prey (rodents) or infected fleas over large distances. Populations of other species associated with prairie ecosystems, such as ferruginous hawks (*Buteo regalis*) and burrowing owls (*Athene cunicularia*), may be adversely affected by the sudden decline in prey base and changes in habitat when rodent populations crash (Antolin *et al.*, 2002). A better understanding of the ecological conditions and species interactions associated with plague is essential to accurately predict plague outbreaks and to enable managers to take timely and appropriate management actions.

### Managing plague in North America

The ability to predict and manage plague outbreaks is important for human health and safety as well as for the protection of valued ecosystems and threatened and endangered species. For example, the long-term survival of the endangered black-footed ferret (*Mustela nigripes*)—perhaps the most endangered mammal in North America—is totally dependent on the wellbeing of its primary prey, prairie dogs, a group of species very susceptible to plague (Antolin *et al.*, 2002). Reducing the occurrence and severity of plague outbreaks would require monitoring rodent, carnivore, and flea populations for the presence of plague, intervening once an outbreak begins or appears imminent, and taking proactive measures to reduce the probability of a plague outbreak (Gage, 1998; Gasper and Watson, 2001).

Several states use serological testing of carnivores as a monitoring tool for plague. In some regions, burrow fleas are monitored regularly to better understand the

dynamics of their populations as well as to determine the presence of plague. A noticeable die-off of rodents can be used as an indicator of a possible plague outbreak. When a die-off occurs, the affected area should be closed to human access, if possible.

At times a plague outbreak can be prevented or slowed by treating rodent burrows with an insecticide such as carbamate or pyrethrin. Unfortunately, the use of insecticides can result in some non-target losses and can have various ecosystem ramifications (Gasper and Watson, 2001). Insecticides should also be applied to people and to pets that are active in rodent-plague areas. The control of rodent populations in and near human habitations is also important to reduce the risk of plague transmission.

Finally, the development and use of effective plague vaccines could greatly reduce the hazards posed by plague to humans, wildlife, and ecosystems. Research is underway to develop an oral plague vaccine for rodents. With an effective and efficient delivery system, such a vaccine could greatly reduce the num-

ber and extent of plague outbreaks.

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